

POPULATION MODELS WITH PARTIAL MIGRATION

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ABSTRACT. Populations exhibiting partial migration consist of two groups of individuals: Those that migrate between habitats, and those that remain fixed in a single habitat. We propose several discrete-time population models to investigate the coexistence of migrants and residents. The first class of models is linear, and we distinguish two scenarios. In the first, there is a single egg pool to which both populations contribute. A fraction of the eggs is destined to become migrants, and the remainder become residents. In a second model, there are two distinct egg pools to which the two types contribute, one corresponding to residents and another to migrants. The asymptotic growth or decline in these models can be phrased in terms of the value of the basic reproduction number being larger or less than one respectively. A second class of models incorporates density dependence effects. It is assumed that increased densities in the various life history stages adversely affect the success of transitioning of individuals to subsequent stages. Here too we consider models with one or two egg pools. Although these are nonlinear models, their asymptotic dynamics can still be classified in terms of the value of a locally defined basic reproduction number: If it is less than one, then the entire population goes extinct, whereas it settles at a unique fixed point consisting of a mixture of residents and migrants, when it is larger than one. Thus, the value of the basic reproduction number can be used to predict the stable coexistence or collapse of populations exhibiting partial migration.

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1. INTRODUCTION

The phenomenon of partial migration, where a population is composed of a mixture of individuals that migrate between habitats and others that remain resident in a single habitat [16], has received extensive attention from biologists seeking to understand its origin and maintenance [5]. Examples of partial migration are diverse and come from nearly every class of organisms. Classic examples include salmonid fishes (*Oncorhynchus*, *Salmo*, and *Salvelinus*) that breed in streams, but contain some individuals that migrate to an ocean or lake and others that complete their entire life cycle in the stream [8], house finches (*Haemorrhous mexicanus*) that share a common breeding site, but some fraction of individuals will migrate away from this site to overwinter [2], and red-spotted newts (*Notophthalmus viridescens*) that breed in a common pond, but a fraction will migrate to the forest to overwinter [9].

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In many cases, migratory and resident individuals can interbreed and produce offspring that can become either migratory or resident [5]. Given the unlikely scenario that migrant and resident forms have equal fitness, one type will have a higher fitness than the other and should "win" the evolutionary competition. Yet, despite this evolutionary intuition, partial migration is maintained in a surprisingly large number of organisms under a wide range of environmental circumstances [5].

A number of mathematical models have been developed to explain the evolution, maintenance, and resulting dynamics of partial migration, and these depend on assumptions such as frequency dependence, density dependence, and condition dependence ([14, 18, 13, 20, 11, 10]). Frequency dependence occurs when a vital rate (survivorship, fecundity, egg allocation strategy) depends on the proportion of individuals in the population adopting a particular strategy. For example, survivorship of migrants might be higher when migrants are rare relative to residents. Density dependence occurs when a vital rate depends on the total number of individuals within a stage or class, resulting in a non-linear relationship between numbers of individuals and population growth. Condition dependence occurs when external factors such as temperature or food availability influence the decision to migrate or not. In particular, density dependence has been identified as an important factor for coexistence of migrants and residents, but it has only been explored in the context of frequency dependence [13, 15]. For example, models that use an evolutionarily stable strategy approach, such as Kaitala and others ([13]), inherently involve frequency dependence among strategy types, in addition to other factors of interest, such as density dependence or condition dependence. Our goal in this paper is to explore the circumstances under which density dependence alone can lead to the stable coexistence of resident and migratory forms.

We based our general model structure on the life history of the salmonid fish *Oncorhynchus mykiss*, which expresses an ocean migratory form (steelhead) as well as a freshwater resident form (rainbow trout). This is an example of 'non-breeding partial migration' [5], in which migrants and residents interbreed in a common habitat. Steelhead and rainbow trout spawn in freshwater streams and their young rear in these streams from one to three years [3]. After this period some individuals will become steelhead and migrate to the ocean and others will remain in the stream as rainbow trout. Using a Leslie matrix model framework based on *O. mykiss*, we assessed conditions for coexistence that do not rely on frequency dependence, but instead rely only on stage-specific density-dependence. Although the model is based on *O. mykiss*, we use the terminology migrants and residents throughout this paper to highlight the applicability of this model framework to many partially migratory species. We prove that a locally defined fitness quantity (R_0) determines the global dynamics of the system, and that there exist stable equilibrium points that allow the coexistence of both resident and migratory forms.

2. LINEAR POPULATION MODELS

We start with a linear stage-structured population model, representing either an isolated population of only migrants or residents with n stages. This is a single-sex model where we are only modeling females. Later we will consider various coupled population models of migrants and residents.

Let x_i denote the number of (female) individuals in stage i , where i ranges from 1 to n . We let t_i be the expected transition probabilities (so that $0 \leq t_i \leq 1$) for individuals from stage i to stage $i + 1$ for $i = 0, \dots, n - 1$, and let t_n denote the survival probability of individuals in the final n th stage. Finally, we let f_i be the fecundities (number of eggs) for $i = 2, \dots, n$. They represent the expected number of offspring produced by an individual in the i th stage.

The dynamics of the number of individuals in the various stages is described by the following Leslie model:

$$(1) \quad \mathbf{x}(t+1) = A_n \mathbf{x}(t),$$

$$\text{with } A_n = \begin{pmatrix} 0 & f_2 & \cdots & f_n \\ t_1 & 0 & \cdots & 0 \\ \vdots & \ddots & \ddots & \vdots \\ 0 & \cdots & t_{n-1} & t_n \end{pmatrix} \text{ and } \mathbf{x} = \begin{pmatrix} x_1 \\ \vdots \\ x_n \end{pmatrix}.$$

We assume that the matrix A_n is irreducible, or equivalently that all $t_i > 0$ for $i = 1, \dots, n-1$, and that $f_n > 0$ [4]. The asymptotic behavior of the non-negative solutions of (1) is determined by the eigenvalue λ of A_n that has largest modulus. Since A_n is a matrix whose entries are non-negative, the Perron-Frobenius theorem implies that λ is in fact real and non-negative. Consequently, when $\lambda < 1$, all solutions converge to zero, and when $\lambda > 1$, then all solutions eventually grow at exponential rate λ . Unfortunately, calculating λ in terms of the entries of the matrix A_n is generally not possible. However, an associated quantity, known as the **basic reproduction number** R_0 , can be determined explicitly. Letting $\rho(M)$ be the spectral radius of any square matrix M , the basic reproduction number R_0 is defined as [6, 17, 1]:

$$R_0 := \rho(F_n(I - T_n)^{-1}),$$

where the matrices F_n and T_n are obtained from A_n by setting all $t_i = 0$ and all $f_i = 0$ respectively. A straightforward calculation shows that

$$(2) \quad R_0 = t_1 f_2 + t_1 t_2 f_3 + \dots + (t_1 \dots t_{n-2}) f_{n-1} + \frac{t_1 \dots t_{n-1}}{1 - t_n} f_n,$$

and reveals the interesting biological interpretation for R_0 as *the expected total number of offspring contributed to stage 1, generated by a single stage 1 individual over its lifetime*. Although this statement is often taken as the definition of the basic reproduction number in the literature, we remark that this is only possible because the model has only one stage in which new offspring is generated. When there are several stages in which offspring are generated (we will later consider models for which this is the case), this clear biological interpretation for the basic reproduction number is no longer possible.

There is an important connection between λ and R_0 , see [17]: Exactly one of the 3 following scenarios occurs:

$$(3) \quad \begin{cases} 0 \leq R_0 \leq \lambda < 1, \text{ or} \\ \lambda = R_0 = 1, \text{ or} \\ 1 < \lambda \leq R_0. \end{cases}$$

Consequently, the long-term behavior of solutions of (1) can be predicted based on whether R_0 is less than, or larger than 1: If $R_0 < 1$, then all solutions converge to zero, and if $R_0 > 1$, then all solutions eventually grow exponentially. In other words, it does not matter whether we use the value of λ , or the value of R_0 to determine population growth or extinction: the location of either one with respect to the threshold 1, is sufficient to decide this issue. Of course, the fact that R_0 is usually more easily computed than λ , makes it the natural candidate to address this question, and this probably explains why R_0 appears to be a more popular measure than λ in the mathematical population biology literature.

A final remark concerns the sensitivity of both λ and R_0 with respect to the natural demographic model parameters t_i and f_i : Both quantities are increasing with respect to increases in any of these parameters. Indeed, for λ this property is a consequence of the Perron-Frobenius Theorem which says that the spectral radius of a non-negative, irreducible matrix, increases with any of the matrix entries. For R_0 , this property is immediately clear from (2). Thus, from the perspective of a sensitivity analysis, it also does not matter which of the two quantities, λ or R_0 , we consider.

Whereas model (1) represents an isolated population of either migrants or residents, in practice these populations are coupled. In the next few sections we explore how various assumptions about how exactly these populations are coupled affect the long term dynamics of the coupled populations.

2.1. A coupled model with a single egg stage. Here we consider the case where the population is composed of migrants and residents that have n and m stages respectively. The potentially different values n and m reflect the fact that migrants and residents will sometimes reproduce (i.e., spawn) at different ages. In the case of steelhead and rainbow trout, steelhead will migrate to the ocean and remain there for extended periods of time to grow before returning as adults, whereas rainbow trout reach adulthood more quickly [3].

The key feature of this model is the assumption that there is a single pool of eggs to which both spawning migrants and residents contribute. This would be the biological case where an event occurs between the egg and juvenile stage that determines an individual's life history trajectory (i.e., whether they become resident or migrant). This could be a threshold growth value [8], a threshold lipid value [19], or a proximate

cue such as density [21]. A fraction $0 < \phi < 1$ of the eggs become migrants, and the remaining fraction $1 - \phi$ become residents. As before, the transition probabilities between the migrant stages are denoted by t_i^s with $i = 1, \dots, n$ and those between the resident stages by t_j^r with $j = 1, \dots, m$. Similarly, the migrant fecundities are f_i^s with $i = 2, \dots, n$, and the resident fecundities are f_j^r with $j = 1, \dots, m$. We also continue to assume that all t_i^s , and t_j^r , and all f_i^s and f_j^r are positive. The coupled model takes the following form:

$$(4) \quad \mathbf{X}(t+1) = A_1 \mathbf{X}(t),$$

where $A_1 = \begin{pmatrix} 0 & f_2^s & \cdots & f_n^s & f_2^r & \cdots & f_{m-1}^r & f_m^r \\ \phi t_1^s & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \ddots & \vdots & \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & \cdots & t_{n-1}^s & t_n^s & 0 & \cdots & 0 & 0 \\ (1-\phi)t_1^r & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & t_2^r & \cdots & 0 & 0 \\ \vdots & \vdots & \cdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 & \cdots & t_{m-1}^r & t_m^r \end{pmatrix}, \quad \mathbf{X} = \begin{pmatrix} \text{eggs}(x_1) \\ \text{first migrant stage}(x_2) \\ \vdots \\ \text{last migrant stage}(x_n) \\ \text{first resident stage}(x_{n+1}) \\ \vdots \\ \text{last resident stage}(x_{n+m-1}) \end{pmatrix}$

We can associate the basic reproduction number to the coupled system (4), which is defined in the familiar way:

$$R_0^{c1} := \rho(F_1(I - T_1)^{-1}),$$

where F_1 and T_1 are obtained from A_1 by setting all transition probabilities t_i^s and t_j^r , respectively all fecundities f_i^s and f_j^r , equal to zero. Since $0 < \phi < 1$, the matrix A_1 is a non-negative irreducible matrix having a real, nonnegative eigenvalue λ_1 of maximal modulus, and all the remarks about the relationship between λ_1 and R_0^{c1} , mentioned for model (1), are also valid here. In particular, (3) holds when replacing R_0 by R_0^{c1} and λ by λ_1 , and therefore population growth or extinction is determined by the location of either λ_1 or R_0^{c1} with respect to the threshold 1. Another important feature of R_0^{c1} is that it has the usual biological meaning of the expected total number of eggs, generated by a single egg over its lifetime. The remarks about the sensitivity of R_0^{c1} with respect to any of the model's transition probabilities and fecundities continues to hold as well.

The sensitivity of R_0^{c1} with respect to the allocation parameter ϕ is not immediately obvious. Indeed, one of the entries in A_1 's first column increases with ϕ , whereas another decreases. However, it turns out that there is a particularly elegant formula for R_0^{c1} in terms of the basic reproduction numbers associated to an isolated n -stage migrants model and an isolated m -stage resident model. To make this precise, we let R_0^s denote the basic reproduction number of model (1) with A_n^s instead of A_n , in which we replace the f_i by f_i^s , and the t_i by t_i^s . Similarly, we let R_0^r be the basic reproduction number of model (1) with A_m^r (i.e. there are m instead of n stages), and replace the f_j by f_j^r , and the t_j by t_j^r . With this notation, it is not difficult to show that R_0^{c1} is a convex combination of R_0^s and R_0^r with weights ϕ and $1 - \phi$ respectively:

$$(5) \quad R_0^{c1}(\phi) = \phi R_0^s + (1 - \phi) R_0^r$$

Clearly, $R_0^{c1}(\phi)$ is linear function of the allocation parameter ϕ , and consequently, $R_0^{c1}(\phi)$ is always between R_0^s and R_0^r . The maximal and minimal values of $R_0^{c1}(\phi)$ are $\max(R_0^s, R_0^r)$ and $\min(R_0^s, R_0^r)$ respectively, and each is achieved for a single, extreme value of ϕ -namely $\phi = 0$ or 1 - unless $R_0^s = R_0^r$, in which case $R_0^{c1}(\phi)$ is independent of ϕ : $R_0^{c1}(\phi) \equiv R_0^s$ for all ϕ in $[0, 1]$.

These observations imply that generically (i.e. when $R_0^s \neq R_0^r$), there is no value of the allocation parameter ϕ that gives rise to a basic reproduction number R_0^{c1} of the coupled model (4) which is higher than both basic reproduction numbers R_0^s and R_0^r , associated with the models of the isolated migrants and isolated residents respectively. In fact, the maximal R_0^{c1} is achieved for an extreme value of the allocation parameter: when $R_0^s > R_0^r$, the maximum is R_0^s , and it is achieved when $\phi = 1$, which corresponds to the scenario in which all eggs become migrants. Similarly, when $R_0^s < R_0^r$, the maximum is R_0^r , and it is achieved when $\phi = 0$, which corresponds to the scenario in which all eggs become residents.

2.2. A coupled model with two distinct egg stages. The key feature of this model is the assumption that there are two pools of eggs: one pool will become migrants and the other will become residents. This would be the biological case where life history (i.e., migrant or resident) is determined at birth. Spawning adult migrants and residents contribute offspring to each pool of eggs. We let $0 < \phi_s < 1$ be the expected fraction of eggs generated by migrants that enter the migrant egg stage. Hence, $1 - \phi_s$ represents the fraction of eggs generated by migrants that enter the resident egg stage. Similarly, ϕ_r is the expected fraction of eggs generated by residents that enter the resident stage.

We let A_n^s and A_m^r be the system matrices of an isolated n -stage migrant and isolated m -stage resident model, as defined in the previous section, and denote the respective basic reproduction numbers by R_0^s and R_0^r respectively. The coupled model then takes the form:

$$(6) \quad \mathbf{X}(t+1) = A_2 \mathbf{X}(t)$$

with

$$A_2 = \begin{pmatrix} \phi_s * A_n^s & (1 - \phi_r) * B_{n \times m}^r \\ (1 - \phi_s) * B_{m \times n}^s & \phi_r * A_m^r \end{pmatrix}, \quad \mathbf{X} = \begin{pmatrix} \text{eggs that become migrants}(x_1) \\ \text{first migrant stage}(x_2) \\ \vdots \\ \text{last migrant stage}(x_n) \\ \text{eggs that become residents}(x_{n+1}) \\ \vdots \\ \text{last resident stage}(x_{n+m}) \end{pmatrix},$$

where $a * A$ is the matrix obtained from A by multiplying all entries of the first row of A by the scalar a , and not changing the entries of any of the other rows of A . The matrices $B_{n \times m}^r$ and $B_{m \times n}^s$ are rectangular with n rows and m columns, respectively m rows and n columns. The first row of the matrix $B_{n \times m}^r$ is the same as the first row of the matrix A_m^r , and all other rows of $B_{n \times m}^r$ consist of zeros. The matrix $B_{m \times n}^s$ is constructed in a similar way from the matrix A_n^s .

Since A_2 is an irreducible, non-negative matrix, we can associate the basic reproduction number to model (6), which is defined as follows:

$$R_0^{c2} := \rho(F_2(I - T_2)^{-1}),$$

where F_2 and T_2 are obtained from A_2 by setting all transition probabilities t_i^s and t_j^r , respectively all fecundities f_i^s and f_j^r , equal to zero. The matrix A_2 has a real, non-negative eigenvalue λ_2 of largest modulus, and the comments in the previous subsection regarding the relationship between λ_1 and R_0^{c1} carry over to the relationship between λ_2 and R_0^{c2} . The remarks on the sensitivity of λ_2 and R_0^{c2} with respect to the transition probabilities and fecundities carry over as well.

There is one notable difference however, namely that unlike R_0^{c1} , the basic reproduction number R_0^{c2} can not be interpreted biologically as some expected number of eggs generated by a single egg over its lifetime, because here there are two distinct egg stages.

To exhibit the dependence of R_0^{c2} on the allocation parameters ϕ_s and ϕ_r , we note that a straightforward calculation shows that:

$$\begin{aligned} R_0^{c2}(\phi_s, \phi_r) &= \rho \begin{pmatrix} \phi_s R_0^s & (1 - \phi_r) R_0^r \\ (1 - \phi_s) R_0^s & \phi_r R_0^r \end{pmatrix} \\ &= \frac{\phi_s R_0^s + \phi_r R_0^r + \sqrt{(\phi_s R_0^s + \phi_r R_0^r)^2 - 4 R_0^s R_0^r (\phi_s + \phi_r - 1)}}{2}, \end{aligned}$$

which is, in general, not a convex function of (ϕ_s, ϕ_r) in $D = \{(\phi_s, \phi_r) : 0 \leq \phi_r \leq 1, 0 \leq \phi_s \leq 1\}$.

Proposition 2.1. *If $R_0^s = R_0^r$, then $R_0^{c2}(\phi_s, \phi_r)$ is a constant function with value R_0^s .*

If $R_0^s \neq R_0^r$, then $R_0^{c2}(\phi_s, \phi_r)$ has no interior maxima or minima on D . Moreover, for $R_0^r < R_0^s$, $R_0^{c2}(\phi_s, \phi_r)$ attains its maximum R_0^s on any point of the boundary of D where $\phi_s = 1$. For $R_0^s < R_0^r$, $R_0^{c2}(\phi_s, \phi_r)$ attains its maximum R_0^r on any point of the boundary of D where $\phi_r = 1$.

Proof. Case 1: $R_0^s = R_0^r$. In this case, a straightforward calculation shows that $R_0^{c2}(\phi_s, \phi_r) \equiv R_0^s$.

Case 2: $R_0^s \neq R_0^r$. Evaluating the partial derivatives of R_0^{c2} with respect to ϕ_s and ϕ_r yields that

$$\begin{aligned} 2 \frac{\partial R_0^{c2}}{\partial \phi_s} &= R_0^s + \frac{(R_0^s \phi_s + R_0^r \phi_r) R_0^s - 2 R_0^s R_0^r}{\sqrt{(\phi_s R_0^s + \phi_r R_0^r)^2 - 4 R_0^s R_0^r (\phi_s + \phi_r - 1)}} \\ 2 \frac{\partial R_0^{c2}}{\partial \phi_r} &= R_0^r + \frac{(R_0^s \phi_s + R_0^r \phi_r) R_0^r - 2 R_0^s R_0^r}{\sqrt{(\phi_s R_0^s + \phi_r R_0^r)^2 - 4 R_0^s R_0^r (\phi_s + \phi_r - 1)}} \end{aligned}$$

Setting $\frac{\partial R_0^{c2}}{\partial \phi_s} = \frac{\partial R_0^{c2}}{\partial \phi_r} = 0$ and simplifying leads to $R_0^s = R_0^r$. Hence, since by assumption $R_0^s \neq R_0^r$, there cannot be any maxima or minima in the interior of D .

If $R_0^r < R_0^s$, then a simple calculation shows that:

$$(7) \quad R_0^{c2}(\phi_s, \phi_r) = \begin{cases} R_0^s & \text{if } \phi_s = 1 \\ \frac{\phi_r R_0^r + \sqrt{(\phi_r R_0^r)^2 - 4 R_0^s R_0^r (\phi_r - 1)}}{2} & \text{if } \phi_s = 0 \\ \frac{\phi_s R_0^s + \sqrt{(\phi_s R_0^s)^2 - 4 R_0^s R_0^r (\phi_s - 1)}}{2} & \text{if } \phi_r = 0 \\ \frac{R_0^s \phi_s + R_0^r + |\phi_s R_0^s - R_0^r|}{2} & \text{if } \phi_r = 1 \end{cases}$$

From equation (7) we observe that the derivative of the single variable functions $R_0^{c2}(\phi_s, 0)$, and $R_0^{c2}(0, \phi_r)$ are never zero on the interval $(0, 1)$. The values at the boundary points of $(0, 1)$ are given by:

$$(8) \quad R_0^{c2}(\phi_s, \phi_r) = \begin{cases} R_0^s & \text{if } \phi_s = 1 \\ (R_0^s R_0^r)^{1/2} & \text{if } \phi_s = 0, \phi_r = 0 \\ R_0^r & \text{if } \phi_s = 0, \phi_r = 1 \end{cases}$$

Hence the maximum R_0^s is attained on D when $\phi_s = 1$.

If $R_0^r < R_0^s$, it can be shown in a similar way that the maximum of R_0^{c2} on D equals R_0^r and that it is attained when $\phi_r = 1$. ■

This result implies that generically (i.e. when $R_0^s \neq R_0^r$), there is no allocation pair (ϕ_s, ϕ_r) for which the basic reproduction number $R_0^{c2}(\phi_s, \phi_r)$ of model (6) is larger than both reproduction numbers R_0^s and R_0^r , associated to the models of the isolated migrants and isolated residents respectively. The maximal R_0^{c2} is achieved for values of the allocation parameter on the boundary of D : when $R_0^s > R_0^r$, the maximum is R_0^s , and it is achieved for $\phi_s = 1$ and arbitrary values of ϕ_r , which corresponds to the scenario in which all migrant eggs become migrants, regardless of the fraction of resident eggs that become residents. Similarly, when $R_0^s < R_0^r$, the maximum is R_0^r , and it is achieved for $\phi_r = 1$ and arbitrary values of ϕ_s , which corresponds to the scenario in which all resident eggs become residents, no matter which fraction of migrant eggs become migrants. These conclusions are similar to those for the basic reproduction number R_0^{c1} of model (1).

3. NONLINEAR DENSITY-DEPENDENT MODELS

Thus far we have neglected any density-dependent effects. Here we assume that transition and survival probabilities depend on the density in each stage. This may be due to stage-specific competition for resources and/or space. We propose the following n -stage uncoupled model, which may be used to model an isolated migrant or an isolated resident population:

$$(9) \quad \mathbf{x}(t+1) = A(\mathbf{x}(t))\mathbf{x}(t),$$

$$\text{where } \mathbf{x} = \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_n \end{pmatrix}, \quad A(\mathbf{x}) = \begin{pmatrix} 0 & f_2 & \cdots & f_n \\ t_1(x_1) & 0 & \cdots & 0 \\ \vdots & \ddots & \vdots & \vdots \\ 0 & \cdots & t_{n-1}(x_{n-1}) & t_n(x_n) \end{pmatrix},$$

and assume that $t_i(x)$ for $1 \leq i \leq n$, and f_j for $2 \leq j \leq n$ satisfy:

- (A1) $t_i(x)$ is C^1 on \mathbb{R}_+ with $0 < t_i(x) \leq 1$ for all $x \in \mathbb{R}_+$, and t_i is strictly decreasing.
- (A2) The function $s_i(x) := xt_i(x)$ is strictly increasing on \mathbb{R}_+ , and there is a bound $m_i \in \mathbb{R}$ such that $s_i(x) \leq m_i$ for all x .
- (A3) $f_j \geq 0$, and $f_n > 0$.

A common choice for $t_i(x)$ is $\frac{b_i}{1+c_i x}$ such that $s_i(x)$ is the Beverton-Holt function. It satisfies (A1)-(A2) when $0 < b_i \leq 1$ and $c_i > 0$ with $m_i = b_i/c_i$, for $1 \leq i \leq n$.

The linearization of system (9) near the fixed point at the origin is:

$$(10) \quad \mathbf{y}(t+1) = A_0 \mathbf{y}(t),$$

where A_0 is the Jacobian of $A(\mathbf{x})\mathbf{x}$ at the origin: $A_0 := \begin{pmatrix} 0 & f_2 & \cdots & f_n \\ a_1 & 0 & \cdots & 0 \\ \vdots & \ddots & \ddots & \vdots \\ 0 & \cdots & a_{n-1} & a_n \end{pmatrix}$, where $a_i := t_i(0)$ for all i .

By (A1) and (A3), A_0 is non-negative and irreducible. Consequently, as we discussed in the previous sections, we can associate the basic reproduction number R_0 to the model. It is defined as $R_0 := \rho(F_0(I - T_0)^{-1})$ where F_0 and T_0 are obtained from A_0 by setting all $t_i = 0$, and all $f_i = 0$ respectively. Moreover, the largest eigenvalue in modulus λ of A_0 and R_0 are either both greater than one, or both less than one, or both equal to one.

Although R_0 is a locally defined quantity, we will show that it determines the global dynamics of system (9). To prove this we shall apply the Cone Limit Set Trichotomy of [12]. Before stating this important result, we need to introduce some definitions regarding monotone systems.

3.1. Monotone systems. We let \mathbb{R}_+^n be the non-negative cone in \mathbb{R}^n . It consists of all vectors that have non-negative entries. For any x and y in \mathbb{R}^n , we write $x \leq y$ ($x < y$) whenever $y - x \in \mathbb{R}_+^n$ and when also ($x \neq y$). We write $x \ll y$ if $y - x \in \text{Int}(\mathbb{R}_+^n)$.

Definition 3.1. A map $F : \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$ is said to be **monotone** if for $x, y \in \mathbb{R}_+^n$, $x \leq y$ implies that $F(x) \leq F(y)$.

Definition 3.2. A map $F : \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$ is **strongly sublinear** if

$$0 < \lambda < 1, \mathbf{x} \gg 0 \Rightarrow \lambda F(\mathbf{x}) \ll F(\lambda \mathbf{x}).$$

Definition 3.3. For $x, y \in \mathbb{R}_+^n$ with $x < y$, we call $[x, y] := \{z \in \mathbb{R}_+^n : x \leq z \leq y\}$ the order interval with endpoints x and y . A subset of \mathbb{R}_+^n is **order bounded** if it is contained in some order interval.

Definition 3.4. A map $F : \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$ is said to be **order compact** if takes every order bounded set into a precompact set.

Theorem 3.5 (Cone Limit Set Trichotomy). Assume $F : \mathbb{R}_+^n \rightarrow \mathbb{R}_+^n$ is continuous and monotone and has following properties for some integer $r \geq 1$, where $F^r := F \circ \cdots \circ F$ denotes the r -fold composition of F with itself:

- (H1) F^r is strongly sublinear.
- (H2) $F^r(x) \gg 0$ for all $x > 0$.
- (H3) F^r is order compact.

Then precisely one of the following holds for the discrete dynamical system $\mathbf{x}(t+1) = F(\mathbf{x}(t))$:

- (R1) each nonzero orbit is unbounded.
- (R2) each orbit converges to 0, the unique fixed point of F .
- (R3) each nonzero orbit converges to $q \gg 0$, the unique non-zero fixed point of F .

3.2. A density-dependent model for an isolated population.

Theorem 3.6. *Assume that (A1)-(A3) hold, and that for all $i = 1, \dots, n$, the maps s_i are strongly sublinear on \mathbb{R}_+ . If $R_0 < 1$ then the zero fixed point is the only fixed point of the system (9) and it is globally asymptotically stable. If $R_0 > 1$, then system (9) has a unique locally stable positive fixed point which attracts all nonzero orbits.*

Proof. : We will prove that the Cone Limit Set Trichotomy, Theorem 3.5, applies to the system (9). Let $F(x(t)) = A(x(t))x(t)$, and denote $F(x) = (F_1(x), F_2(x), \dots, F_n(x))$, it follows that $F_1(x) = \sum_{i=2}^n f_i x_i$, $F_i(x) = s_{i-1}(x_{i-1})$ for $i = 2 \dots n-1$, and that $F_n(x) = s_{n-1}(x_{n-1}) + s_n(x_n)$. First, we will show that $F(x)$ satisfies the hypotheses (H1) - (H3). Each s_i is strictly increasing by (A2), and therefore F is monotone on \mathbb{R}_+^n . Clearly, F is continuous as well.

Remark that F is not strongly sublinear because $\lambda F_1(x) - F_1(\lambda x) = 0$ for $0 < \lambda < 1$ and all x . Thus, we consider F^2 , and we note that $F_1^2(x) = f_n s_n(x_n) + \sum_{i=2}^n f_i s_{i-1}(x_{i-1})$, $F_2^2(x) = s_1(\sum_{j=2}^n f_j x_j)$, $F_i^2(x) = s_{i-1} \circ s_{i-2}(x_{i-2})$, $i = 3, \dots, n-1$, and $F_n^2(x) = s_{n-1} \circ s_{n-2}(x_{n-2}) + s_n \circ (s_{n-1}(x_{n-1}) + s_n(x_n))$. It is easy to verify that the composition of any two functions s_i , is strongly sublinear because each s_i is strictly increasing by (A2) and strongly sublinear by assumption. It follows that F^2 is strongly sublinear because each coordinate function F_i^2 is a positive linear combination of strongly sublinear functions, hence strongly sublinear as well. A similar argument shows that F^r is also strongly sublinear for any $r \geq 2$.

It follows from (A1) and (A2) that $s_i(x_i) > 0$ for all $x_i > 0$ and all $i = 1, \dots, n$. This property and the fact that $f_n > 0$ by (A3) imply that $F^n(x_0) \gg 0$ whenever $x_0 > 0$.

Since F^n is a continuous function on a finite dimensional space, it is order compact.

In summary, we have shown that F satisfies hypotheses (H1)-(H3) of the Cone Limit Set Trichotomy for $r = n$.

From the above calculation of the coordinate functions, it follows that F^2 maps \mathbb{R}_+^n into the order interval $[0, a]$, where

$$a := \begin{pmatrix} f_n m_n + \sum_{i=2}^n f_i m_{i-1} \\ m_1 \\ m_2 \\ \vdots \\ m_{n-1} \\ m_{n-1} + m_n \end{pmatrix}$$

Since F is continuous, $F([0, a])$ is compact, and therefore all orbits of system (9) are bounded, hence also order bounded. In particular, (R1) does not hold for system (9). Therefore, either (R2) or (R3) must hold, and we show next that which particular case occurs, depends on the value of R_0 .

Case 1: $R_0 < 1$.

In this case we will show that (R3) does hold for F . Here, $\lambda = \rho(A_0) < 1$ because $R_0 < 1$, and thus $A_0^t \rightarrow 0$ as $t \rightarrow +\infty$. Let $x(t)$ be the solution of (9) with initial condition $x(0) > 0$. We observe that $A(x) \leq A_0$ for all $x \geq 0$, where the matrix inequality is understood to hold entry-wise. This implies that $x(t) \leq A_0^t x(0) \rightarrow 0$ as $t \rightarrow +\infty$, and therefore also $x(t) \rightarrow 0$ as $t \rightarrow +\infty$. In summary, if $R_0 < 1$, then system (9) has a unique fixed point at the origin which attracts all orbits, by (R2) of Theorem 3.5.

Case 2: $R_0 > 1$.

In this case we will show that (R2) does not hold for F . Here, $\lambda = \rho(A_0) > 1$ because $R_0 > 1$. By the Perron-Frobenius Theorem, A_0 has a positive eigenvector v corresponding to the eigenvalue λ . Set $x_0 = \epsilon v$ for some small $\epsilon > 0$ to be determined momentarily. Using the Taylor expansion of F near the origin, we have that $F(x_0) = \epsilon A_0 v + O(\epsilon^2) = \epsilon \lambda v + O(\epsilon^2)$. Therefore, $F(x_0) - x_0 = \epsilon v(\lambda - 1) + O(\epsilon^2) \gg 0$ for all sufficiently small $\epsilon > 0$. Monotonicity of F then implies that $x_0 < F(x_0) \leq F^2(x_0) \leq \dots$, and hence the orbit of x_0 does not converge to 0. By Theorem 3.5, it follows that system (9) has a unique positive fixed point, which attracts all nonzero orbits. ■

3.3. A coupled density-dependent model with a single egg stage. We consider the following density-dependent coupled model of a n -stage migrant and a m -stage resident population:

$$(11) \quad \mathbf{X}(t+1) = A_1(\mathbf{X}(t))\mathbf{X}(t),$$

where $A_1(\mathbf{X}) = \begin{pmatrix} 0 & f_2^s & \cdots & f_n^s & f_2^r & \cdots & f_{m-1}^r & f_m^r \\ \phi t_1^s(x_1) & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \ddots & \vdots & \vdots & \vdots & \cdots & \vdots & \vdots \\ 0 & \cdots & t_{n-1}^s(x_{n-1}) & t_n^s(x_n) & 0 & \cdots & 0 & 0 \\ (1-\phi)t_1^r(x_1) & 0 & \cdots & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & t_2^r(x_{n+1}) & \cdots & 0 & 0 \\ \vdots & \vdots & \cdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 & \cdots & t_{m-1}^r(x_{n+m-2}) & t_m^r(x_{n+m-1}) \end{pmatrix},$

and

$$\mathbf{X} = \begin{pmatrix} \text{eggs}(x_1) \\ \text{first migrant stage}(x_2) \\ \vdots \\ \text{last migrant stage}(x_n) \\ \text{first resident stage}(x_{n+1}) \\ \vdots \\ \text{last resident stage}(x_{n+m-1}) \end{pmatrix}$$

Here, $\phi \in (0, 1)$ represents the fraction of eggs from the common egg pool that will enter the first migrant stage, and hence $1 - \phi$ is the fraction that will enter the first resident stage. The fecundities f_i^s and f_j^r and transition probability functions $t_1^s(x_1)$, $t_i^s(x_i)$ and $t_1^r(x_1)$, $t_j^r(x_{n+j-1})$ for $i = 2, \dots, n$ and $j = 2, \dots, m$ are assumed to satisfy the hypotheses (A1)-(A3) of two respective models of the form (9), one for migrants and another for residents, for which we are using the functions $s_i^s(x) = xt_i^s(x)$ for $i = 1, \dots, n$ and $s_j^r(x) = xt_j^r(x)$ for $j = 1, \dots, m$. To each model we also associate a basic reproduction number as in the previous subsection, and denote these as R_0^s and R_0^r .

The Jacobian $A_{1,0}$ of system (11) at the origin is obtained from $A_1(\mathbf{X})$ by replacing $t_i^s(x_i)$ with $t_i^s(0)$ for $i = 1, \dots, n$ and $t_j^r(x_j)$ with $t_j^r(0)$ for $j = 1, \dots, m$. The matrix $A_{1,0}$ is non-negative and irreducible, and we can associate a basic reproduction number to the linearized system, defined as $R_0^{1c} = \rho(F_0^1(I - T_0^1)^{-1})$ where F_0^1 and T_0^1 are obtained from $A_{1,0}$ by setting respectively all $t_i^s = t_j^r = 0$, and all $f_i^s = f_j^r = 0$. Note that in particular, the relationship (5) between the basic reproduction numbers associated to the coupled model, R_0^{1c} , and the two isolated models, R_0^s and R_0^r , continues to hold in this context. Similarly, the sensitivity properties of R_0^{1c} with respect the parameters of the linearized system, and in particular the remarks concerning the location of the maximum of R_0^{1c} , when considered as a function of ϕ , as discussed in subsection 2.1, remain valid here as well.

We also have the following global stability result for the coupled system (11).

Theorem 3.7. *Assume that (A1)-(A3) hold for each of the two isolated population models. Assume also that the maps s_i^s and s_j^r are strongly sublinear on \mathbb{R}_+ for all $i = 1, \dots, n$ and all $j = 1, \dots, m$. If $R_0^{1c} < 1$, then the origin is the unique fixed point of system (11) and it is globally asymptotically stable. If $R_0^{1c} > 1$, then system (11) has a unique locally stable positive fixed point which attracts all nonzero orbits.*

Proof. We apply Theorem 3.5 to system (11). Let $G(\mathbf{X}) = A^1(\mathbf{X})\mathbf{X}$ be obtained from system (11). Letting $G(\mathbf{X}) = (G_1(\mathbf{X}), G_2(\mathbf{X}), \dots, G_{n+m-1}(\mathbf{X}))$, we have more explicitly that $G_1(\mathbf{X}) = \sum_{i=2}^n f_i^s x_i + \sum_{i=2}^{m+n-1} f_i^r x_i$, $G_2(\mathbf{X}) = \phi s_1^s(x_1)$, $G_i(\mathbf{X}) = s_{i-1}^s(x_{i-1})$ for $3 \leq i \leq n-1$, $G_n(\mathbf{X}) = s_{n-1}^s(x_{n-1}) + s_n^s(x_n)$, $G_{n+1}(\mathbf{X}) = (1-\phi)s_1^r(x_1)$, $G_{n+j}(\mathbf{X}) = s_j^r(x_{n+j-1})$ for $2 \leq j \leq m-2$ and $G_{n+m-1}(\mathbf{X}) = s_{m-1}^r(x_{n+m-2}) + s_m^r(x_{n+m-1})$.

All $G_k(\mathbf{X})$ are either linear functions, or nonnegative linear combinations of strongly sublinear functions s_l^s or s_q^r . The rest of the proof is then similar to the proof of Theorem 3.6. \blacksquare

3.4. A coupled density-dependent model with two distinct egg stages. A density-dependent coupled nonlinear model can be obtained from the linear model (6) in which the transition probability constants t_i^s are replaced by functions $t_i^s(x_i)$ for $i = 1, \dots, n$, and the constants t_j^r are replaced by functions $t_j^r(x_{n+j})$ for $j = 1, \dots, m$. The coupled dynamics between an n -stage migrant and an m -stage resident population is then given by:

$$(12) \quad \mathbf{X}(t+1) = A_2(\mathbf{X}(t))\mathbf{X}(t),$$

$$\text{with } A_2(\mathbf{X}) = \begin{pmatrix} \phi_s * A_n^s(\mathbf{X}) & (1 - \phi_r) * B_{n \times m}^r(\mathbf{X}) \\ (1 - \phi_s) * B_{m \times n}^s(\mathbf{X}) & \phi_r * A_m^r(\mathbf{X}) \end{pmatrix}.$$

Here, the allocation parameters ϕ_s and ϕ_r belong to the interval $(0, 1)$, and have the same interpretation as in subsection 2.2. Also, the submatrices in $A_2(\mathbf{X})$ are defined in a similar way as in model (6), although here the transition probabilities are functions of the state rather than constants due to density dependence (fecundities remain constants). Again we assume that all transition probability functions and fecundities satisfy the hypotheses (A1)-(A3) as in two associated models of the form (9), one for migrants and one for residents, and where $s_i^s(x) = x t_i^s(x)$ for $i = 1, \dots, n$ and $s_j^r(x) = x t_j^r(x)$ for $j = 1, \dots, m$. To each of these models we also associate a basic reproduction number based on the linearization at the origin, in the same way as in the previous subsection. We denote these as R_0^s and R_0^r .

To the coupled model (12), we also associate a basic reproduction number R_0^{c2} , based on the linearization at the origin. The relation between R_0^{c2} on one hand, and R_0^s and R_0^r on the other, as discussed in subsection 2.2, remains valid here as well.

The global behavior of system (12) is as follows:

Theorem 3.8. *Assume that (A1)-(A3) hold for each of the two isolated population models. Assume also that the maps s_i^s and s_j^r are strongly sublinear on \mathbb{R}_+ for all $i = 1, \dots, n$ and all $j = 1, \dots, m$. If $R_0^{c2} < 1$ then the fixed point at the origin is the only fixed point of system (12), and it is globally asymptotically stable. If $R_0^{c2} > 1$, then system (12) has a unique positive locally stable fixed point which attracts all nonzero orbits.*

Proof. Yet again, the proof of this theorem is an application of Theorem 3.5. Let $H(\mathbf{X}) = A_2(\mathbf{X})\mathbf{X}$. With $H(\mathbf{X}) = (H_1(\mathbf{X}), H_2(\mathbf{X}), \dots, H_{m+n}(\mathbf{X}))$, we have that $H_1(\mathbf{X}) = \phi_s(\sum_{i=2}^n f_i^s x_i) + (1 - \phi_r)(\sum_{i=n+2}^{2n} f_i^r x_i)$, $H_i(\mathbf{X}) = s_{i-1}^s(x_{i-1})$, for $2 \leq i \leq n-1$, $H_n(\mathbf{X}) = s_{n-1}^s(x_{n-1}) + s_n^s(x_n)$, $H_{n+1}(\mathbf{X}) = (1 - \phi_s)(\sum_{i=2}^n f_i^s x_i) + \phi_r(\sum_{i=n+2}^{m+n} f_i^r x_i)$, $H_{n+j}(\mathbf{X}) = s_j^r(x_{n+j})$, for $2 \leq j \leq m-1$, and $H_{m+n}(\mathbf{X}) = s_{m-1}^r(x_{m+n-1}) + s_m^r(x_{m+n})$.

The coordinate functions $H_i(\mathbf{X})$ of $H(\mathbf{X})$ are either linear functions, or non-negative linear combinations of strongly sublinear functions s_i^s or s_j^r . The rest of the proof is then similar to the proof of Theorem 3.6. ■

4. CONCLUSION

We developed four models of partial migration with the example of salmonid fishes in mind. The models address the cases of one pool of eggs (with a fraction becoming migrant and the rest resident) and two pools of eggs (one pool becomes migrant and the other resident), with and without density dependence. The evolutionary decision to become migratory or resident can take place at the egg stage or juvenile stage. We found that in the absence of density dependence that asymptotic growth in these models is governed by the value of the basic reproduction number. Under density dependence, the asymptotic dynamics are also governed by the value of a locally defined basic reproduction number, which determines whether the population goes extinct or settles at a unique fixed point consisting of a mixture of migrants and residents. Whether migration is determined at the egg or juveniles made no difference in the asymptotic dynamics between models. Our analysis shows that the basic reproduction number alone can be used to predict the stable coexistence or collapse of populations with partial migration. One result of our analyses is that population persistence of both migrant and resident forms can occur with density dependence alone. However, our analysis did not consider this persistence in the context of evolution, in which new strategies that involve different allocation to resident and migrant forms can invade the population. This question could be addressed with future research involving methods such as adaptive dynamics [7].

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